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Word Count = 10 759

Keywords = pair-bond, zebra finch, acoustic communication, social network, group collective calling, turn-taking, vocalizations, songbird.

Abstract

In social species individuals living in the same group may synchronize activities such as movements, foraging or anti-predator vigilance. Synchronization of activities can also be observed between partners especially during breeding and can be crucial for breeding success. Vocalizations are behaviours that can be coordinated between individuals, but simultaneous vocalizations in groups have most of the time been considered as a noise that does not bear any information.

Indeed little is known about the structure and function of vocal communications involving a network of individuals. How the individual vocal activity participates in the resulting communal sound, and in return how the group influences individual vocal activity, are questions that remain to be studied. Zebra finches are social monogamous songbirds that form lifelong pair-bonds. In the wild, zebra finches are typically found in small groups, with the pair as the primary social unit, and gather in 'social' trees where both females and males produce vocalizations. Here we investigated in the laboratory the influence of group size and composition on general vocal activity and synchrony, as well as the influence of pair-bond and spatial location on finer characteristics of dyads vocal interactions. We used a set-up that locked the birds at fixed spatial positions of our choosing to control the proximity network and allowed us an individual tagging of most of the vocalizations. We used an in-house software suite that automatically detects vocalizations from hours of passive recording.

We show that zebra finches groups synchronize their general vocal activity with waves of collective vocalizations, which depend both on the group size and composition. The acoustic network is shaped by pair-bonds at different time scales. Birds preferentially vocalize closely in time (synchrony) or directly after (turn-taking) their partner when it is present and then the nearest neighbour when the partner is not available.

Introduction

In social species, many activities are synchronized between individuals living in the same group. Group members maintain group cohesion during movements and foraging (Agetsuma, 1995; Beauchamp, 1992; Blanc & Thériez, 1998; Blanc, Thériez, & Brelurut, 1999; Boyd & Bandi, 2002; Chivers, 1974; Conradt, 1998; Côte, Schaefer, & Messier, 1997; Daan & Slopsema, 1978; Gillingham & Klein, 1992; Linnane, Brereton, & Giller, 2001; McMahon & Evans, 1992; Rasmussen, 1985; Rook & Huckle, 1995; Ruckstuhl, 1998, 1999; Ruckstuhl & Neuhaus, 2001; Saino, Fasola, & Waiyaki, 1995; Schenkeveld & Ydenberg, 1985; Tayler, 1953; Tremblay & Cherel, 1999; Wilson, Wilson, & McQuaid, 1986). Individuals may also coordinate activities such as anti-predator vigilance and feeding (Gerkema & Verhulst, 1990; Kavanagh, 1978; Rook & Penning, 1991). Activities can also be synchronized between partners of a pair. Pairs in many long-term monogamous species show an increase in their breeding success over time, and this could be attributed to a better coordination of partners (Black & Hulme, 1996; Forslund & Pärt, 1995). Partners can also coordinate foraging activities, and can synchronize their nest visits to feed the chicks (Bebbington & Hatchwell, 2015; Lee, Kim, & Hatchwell, 2010; Mariette & Griffith, 2012, 2015; van Rooij & Griffith, 2013). When both partners incubate, their hatching success can increase by synchronizing foraging trips (Coulson, 1966; Davis, 1988) or coordinating incubation bouts (Spoon, Millam, & Owings, 2006).

Vocalizations are behaviours that can be coordinated between individuals. Territorial songbirds vocally compete by answering each other, sometimes matching their song-types and using song-overlap as a signal of escalation (Langemann, Tavares, Peake, & McGregor, 2000). Some monogamous birds use coordinated vocal duets for territory defense, mate guarding, pair-bond maintenance (Farabaugh, 1982; Hall, 2004) or parental care (Boucaud, Mariette, Villain, & Vignal, 2015; Elie et al., 2010). Some group vocal productions have also been identified as organized signals bearing messages, like the communal vocalizations of some social mammals that communicate on spacing (Bornean gibbons, *Hylobates muelleri*, (Mitani, 1984); wolves, *Canis*

lupus, (Harrington & Mech, 1979); (Frommolt, 1999)) or group size (female lions, *Leo leo*, (McComb, Packer, & Pusey, 1994). But most of the time, group vocal productions have been considered as by-products of individuals' simultaneous but not necessarily coordinated vocalizations. For example, this noisy sound can result from the activity of up to thousands of individuals in choruses of birds (Burt & Vehrencamp, 2005), insects (Greenfield, 1994), frogs (M. E. Bates, Cropp, Gonchar, & Knowles, 2010; Jones, Jones, & Ratman, 2009; Marshall, 2003; Simmons, Bates, & Knowles, 2009), as well as in fish communities (D'spain & Berger, 2004; Locascio, 2004; Locascio & Mann, 2005; Mann, 2003), colonies of nesting birds (Adret-Hausberger, 1982; Mathevon, 1997) or breeding marine mammals (Schusterman, 1978; Southall, Schusterman, & Kastak, 2003). This sound resulting from a group of individuals vocalizing simultaneously has mainly been viewed as a source of noise pollution constraining the pairwise communications (Aubin & Jouventin, 1998; Gerhardt & Klump, 1988). But this group sound with no clear identifiable message might bear information on the structure of the underlying social network (McGregor & Horn, 2014).

Not much is known about the structures and functions of vocal communications involving a network of individuals. More specifically, little is known about the dynamics of pairs and group vocal exchanges at an individual-level resolution. How the individual vocal activity participates in the resulting communal sound, and in return how the group influences individual vocal activity, are questions that remain to be studied. Yet, we know that the group, as a communication network, is composed of several signalers and receivers sharing the same active signaling space, which implies that it can interfere with pairwise vocal exchanges. Eavesdropping is defined as extracting information from signaling interactions while not being the main recipient, and seems to occur in many species (McGregor & Dabelsteen, 1996). In birds for example, it has been shown that eavesdroppers can respond to vocal exchanges even if they were not part of it initially (Mennill, Ratcliffe, & Boag, 2002). Audience effects show that the presence of other conspecifics can

influence a sender's behavior (Doutrelant, McGregor, & Oliveira, 2001; Evans & Marler, 1994; Hector, Seyfarth, & Raleigh, 1989; Matos & McGregor, 2002; Plath, Blum, Schlupp, & Tiedemann, 2008). The communication behaviour of male zebra finches can be modified by the individuals that are listening, and by the nature of the social relationships between them (Vignal, Mathevon, & Mottin, 2004).

The zebra finch (*Taeniopygia guttata*) is a social species native to Australia and is monogamous. This songbird forms lifelong pair-bonds (Zann, 1996), and partners are inseparable even outside of the breeding season. In the wild, zebra finches are usually found in small groups, and the pair is the primary social unit (McGowan, Mariette, & Griffith, 2015). This species extensively uses acoustic communication during social interactions: groups gather in 'social' trees near watering points or feeding areas (Zann, 1996) in which they produce a background sound composed of calls and songs. Some studies have started to focus on vocal dynamics in this species (Elie, Soula, Mathevon, & Vignal, 2011; Fernandez, Mariette, Vignal, & Soula, 2016; Gill, Goymann, Ter Maat, & Gahr, 2015; Perez, Fernandez, Griffith, Vignal, & Soula, 2015; Villain, Fernandez, Bouchut, Soula, & Vignal, 2016). Because of the amount of accumulated knowledge on both behavioral and neurobiological aspects of its acoustic communication, the zebra finch is an interesting model to study communal vocalization and its relation to the social structure of the group.

Here we hypothesized that the organization of group vocal activity might reveal some aspects of group structure, such as group size and composition. Using the zebra finch as a study species, we investigated the impact of group size and composition on proxies of the group vocal activity and synchrony. We also tested the influence of pair-bonds and spatial location on finer characteristics of dyads vocal interactions. One common difficulty encountered when studying an acoustic network is to determine the identity of the caller and thus to obtain an individual tagging of vocalizations. Also, when we want to assess the acoustic network it might be relevant to control

105 the spatial proximity between individuals. To overcome both of these issues we used a set-up that
106 first locked the birds in a fixed spatial network of our choosing and allowed us an individual tagging
107 of all vocalizations. We used an in-house software suite that automatically detects vocalizations
108 from hours of passive recording. Our setup also allows for an automatic removal of non-
109 vocalizations (wings or cage noise) using classification.
110 We built groups of identical sex-ratio but that varied in group sizes and social structures
111 (percentage of paired / unpaired birds). We recorded these groups' vocal activity during several
112 hours on several days, and analyzed the vocal sequences resulting from these recordings.

Materials and Methods

Subjects and Housing Conditions

We used 88 adult zebra finches (*Taeniopygia guttata*) in this study: 44 males and 44 females. All birds came from our breeding colony. Before the experiment, unpaired males and unpaired females were housed with individuals of the same sex, and female-male pairs were housed separately in cages (all cages dimensions: 40 X 40 X 40 cm) equipped with perches and a pool for environmental enrichment. All birds were kept under the same environmental conditions: temperature between 24 and 26 °C, light conditions of 14:10 h light-dark, water, seeds and cuttlefish bones ad libitum and supplemented with salad once a week. As zebra finches are opportunistic breeders, all conditions were reunited for them to breed (water restriction is needed to be in non-breeding condition (Prior, Heimovics, & Soma, 2013). However they did not have access to nest material so they were not breeding at the time of the recording.

Recording Protocol

The experiment took place from March to May 2014 and from January to February 2015. The day before the experiment, each bird was moved from the rearing room to the experimental room (sound attenuating chamber, 2.22 m height x 1.76 m width x 2.28 m length, Silence Box model B, Tip Top Wood, France) and was placed in a cage (40 X 40 X 25). Microphones (Audio Technica AT803), connected to a recorder (zoom R16), were placed on top of each cage, above the head of the bird and facing downwards, which is the best position to minimize the variability in vocalization amplitude due to the orientation of the bird's head, and thus maximize vocalization detection (Brumm & Zollinger, 2011). On each recording day, we recorded vocal exchanges during a long period (three to six hours between 10 am and 4 pm).

Group Composition

We recorded 35 groups of different sizes (two, four, or eight individuals) and different social compositions (0%, 50%, or 100% of paired birds). Table 1 gives the number of recorded groups per group size and composition, as well as the number of repetitions for each group, and the total number of hours of recording for each combination. We organized the cages so that all birds can be in visual contact with each member of the group (Figure 1). We defined the distance between two birds as one if the two birds' cages were neighbour, two if the two birds' cages were separated by one cage, etc. Pair mates were always put in neighbouring cages to reduce stress. In 4-bird groups, two males were always located in diagonal and two females in diagonal. In 8-bird groups, the positions of males and females were defined at random.

Vocalization Extractions

Vocalizations were extracted from recordings using in-house softwares. These programs were written in python (www.python.org) by authors H.A.S. and M.S.A.F using open-source libraries.

Briefly, vocalization detection consisted of a pipeline of five stages. The first process was a simple threshold-based sound detection based on a high-pass filtered energy envelope (1024 samples FFT; 441 Hz sampling; cut-off frequency: 500Hz). During the second stage, each event above the threshold was reconstructed in order to maintain an amplitude range of 90% compared to the maximum amplitude. Thus, each event was either lengthened or shortened to obtain the same amplitude range during the event. This technique allows a good estimate of a vocal event's duration. The third stage simply merged overlapping event segments. Together, the three first stages produced start, end, and duration values for each sound event detected in the recording. The accuracy of these three first steps was tested in (Elie et al., 2011).

The fourth stage removed double vocalizations - vocalizations produced by one bird and recorded by its microphone but also recorded by the microphones of all other birds of the group - by using energy and delay differences: to attribute a vocalization to a bird, our program detects vocalizations for each microphone. Then we apply the following algorithm: for each vocalization A (start=sA, end=eA) we look if other vocalizations were detected at the same period in other microphones. If for a vocalization B (start = sB) we have sB>sA but sB<eA (B is starting after A but is overlapping A) we look if the energy of vocalization B is higher than the energy of A. If this is the case we keep both vocalizations. If not, we remove B (because B is likely to be A recorded in another microphone). We do this for all vocalizations by eliminating them and/or associate them with a track (hence a bird). Thus, when a vocalization was produced without overlap with another vocalization, our program has a success rate of 100 % (see corresponding tests in supplementary figure 1, a human listener would make more mistakes because the time delay between two microphones is very low, i.e. few milliseconds). The main problem occurs when a vocalization B overlaps a vocalization A (sB<eA), and when B is weaker on its microphone B than A is on the microphone A. In that case our program considers that B is the same vocalization as A, and thus the vocalization B is lost. We have quantified this type of error. The overlapping vocalizations represent around 11% of the total number of vocalizations. We have a 46% error rate on overlapping vocalizations, i.e. the software makes a mistake when attributing the overlapping vocalizations in 46% of the cases (percentages computed over 1200 vocalizations over eight randomly chosen groups). Thus the errors due to overlapping vocalizations increases the final error rate by 5%.

This step effectively tagged uniquely each sound event to an individual. The fifth and last stage removed cage or wings noises using a machine learning process. We trained a supervised classifier using a data set composed of 4500 random extracted sounds from all of our data. Each sound was classified by one expert (M.S.A.F.) as “vocalization” or “non- vocalization”. The classification was performed on the spectrogram of the sounds reduced to 50ms: the idea was to

reduce the quantity of information in term of time and frequency, and sample this information in such a way that we got the same amount of information for each vocalization (short or long). The spectrogram matrix was first reduced to the frequencies of interest – between 500Hz and 6kHz. Then two cases appeared: if the vocalization duration was longer than 50 ms, we extracted 50 ms in the middle of the sound event. If duration was lower than 50 ms, we padded with zero to obtain a 50ms sound event with the relevant event in the middle. The spectrogram was then flattened to obtain a one dimensional vector. We trained a Random Forest classifier (Breiman, 2001) using 1500 sounds as a training set. The validation set was composed of the remaining 3000 sounds. This classifier had an overall rate of error below 10%.

Our vocalization extraction yielded over 1,730k vocalizations (840k for females and 890k for males) over a total of 441 hours of recording. Supplementary Figures 2(a) and 2(b) show the histograms of vocalization durations for all extracted vocalizations for each sex. These distributions are composed of two modes that likely represent the two main types of vocalizations produced by zebra finches in this context (Zann, 1996): distance calls i.e. the longer and louder calls given by zebra finches, consisting of a harmonic series modulated in frequency as well as amplitude, and tet or stack calls i.e. softer and shorter calls than distance calls, around 50ms (Zann, 1996). Song syllables are also represented in this histogram because they could not be removed from the dataset (see above). We estimated several parameters of the distribution using a sum of two Gaussians:

$$P(d) = a\,N(\mu_1, \sigma_1^2) + (1-a)\,N(\mu_2, \sigma_2^2)$$

where $N(\mu, \sigma^2)$ is the normal Gaussian distribution with mean μ and variance σ^2. The fit was made on the duration histogram (time step=10ms on 0-1s interval) with the least square method.

Note that individual song syllables (for males) are not discriminated in one category and can be of any duration. Female and male short calls (tet or stack) have similar duration (first mode at 52 ms).

Consistent with the literature, distance calls are shorter in males (120 ms) compared to females (149 ms) (Supplementary Table 1).

Because we were interested only in the dynamic of the vocal exchanges, we decided to pool all vocalizations types together in the following analyses.

Data Analysis

We separated the analysis into four parts described below: general vocal activity and vocalization rate autocorrelation (analysis of long-term vocal dynamics), and the dyads cross-correlation and turn-taking transitions analysis (analysis of short-term vocal dynamics).

General vocal activity

We computed the main vocal activity metrics namely the number of vocalizations per time unit for each individual. We also defined a burst as a period where the total vocal activity (for all individuals in the group) was 10% higher than the average vocal activity (taken on the whole recording day). To find the bursts we split the time into six minutes bins with an overlap of one minute. Thus, a burst could not last less than 5min. We then analyzed the number of bursts per hour and the total vocalizations rate in bursts only.

Vocalization rate autocorrelation

The vocalization rate autocorrelation gives information about the presence of cycles in the group general vocal activity. For example, it could tell if the variation of vocalization rate presents patterns over time, i.e. waves of collective vocalizations.

We split the time into 180s bins (3min) with an overlap of 90s (1min30) and counted the total number of vocalizations in each bin. We then computed the autocorrelation AC(T) of this signal with the following formula:

$$ac(T) = mean[(S(t) - mean(S))(S(t+T) - mean(S))],$$

with the normalization step we have: $AC(T) = ac(T)/ac(0)$. t is the time bin number, S(t) is the total number of vocalizations in the bin t, and T is the time lag value, between 0 and 80 min.

A peak at time T in the autocorrelation curve means that the vocalization rate activity presents a cycle of duration T.

Cross-correlation

We assessed the vocal temporal synchrony between two birds by computing the cross-correlation at T=500 ms. To do that we split the time into 500 ms bins, and each bird signal was one if the bird vocalized within this period, and zero if not. We computed the cross-correlation (CC(T)) of the two birds' signals with the following formula:

$$cc = mean[(S_{bird1}(t) - mean(S_{bird1}))(S_{bird2}(t) - mean(S_{bird2}))],$$

with the normalization step we have: $CC(T) = cc(t) / (SD(S_{bird1})* SD(S_{bird2}))$

Where S_{bird1} and S_{bird2} the two birds vocal signals as functions of t (time).

For each day of recording we computed cross-correlations for all possible dyads of birds. Two birds having a high cross-correlation value were two birds that were regularly vocalizing closely in time together (within 500ms).

We compared cross-correlation between paired/unpaired and neighbour/non-neighbour birds.

Turn-taking transitions probability

In this analysis, we kept only the sequence of callers' identity (without temporal aspect), i.e. the turn-taking. Vocal sequences were obtained with the caller's identity in their order of vocalizing (e.g. ABCA was a sequence of four vocalizations, produced successively by the bird A, then bird B, bird C and finally bird A). We compared the mean transition probabilities for each dyad of birds: between bird A and bird B, the mean transition probability is (prob(A->B)+prob(B->A)) / 2. We compared this measure between paired/unpaired and neighbour/non-neighbour birds.

Statistics

All statistical tests were performed using R software (R Core Team, 2014). Linear mixed models were built with the lmer function ('lme4' R package (D. Bates, Maechler, Bolker, & Walker, 2014)) and generalized mixed models were built with the glmer function ('lme4' R package). Models outputs from Anova ('car' library) and summary functions are presented.

Model validation

Before being interpreted each model was checked, paying particular attention to their residuals. For models with Poisson family, overdispersion was tested, and if the model presented overdispersion we used a negative binomial model. The model validity was also checked with the plotresid function from the 'RVAideMemoire' package before interpreting the model results. When possible, the variance of the data explained by the models was quantified and a conditional coefficient of determination was calculated with 'r.squaredGLMM' function ('MuMIn' R package).

Model selection

We chose to build biologically relevant models and we kept the full model as recommended by Forstmeier & Schielzeth (2011).

Model estimates and confidence intervals

When possible we added information about the quantification of the biological effect given by the models. Confidence intervals were computed with the "confint.merMod" function of the lme4 package, with the Wald method.

Vocal activity

- Number of vocalizations

We chose to use the number of vocalizations (NVoc) as the response variable (seen as a count) and we added the recording duration (RecordingDuration) as an offset because all recordings did not last the same time. It was not possible to test the interaction between the group size (GroupSize) and the percentage of pairs in the group (PercentPair) because by definition we did not have a complete crossover design. The other interactions were tested because they were biologically relevant (BirdSex * GroupSize and BirdSex * PercentPair). As a bird could be recorded in several groups, we added the random factor GroupID/BirdID (group identity / bird identity), which took into account the group and the bird in the group. We also had repetitions of recording for each group so we added the repetition number (RepetitionNb) as a random factor:

NVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair), random=GroupID/BirdID, RepetitionNb

We used a negative binomial model as the model using a Poisson distribution presented over-dispersion. The interaction between BirdSex and GroupSize was significant, so we separated the dataset into three subsets (for the three group sizes).

- Number of bursts: We counted the number of bursts and tested the influence of the group size and percentage of pairs on this metric. We built a generalized Poisson model with the recording duration as offset. As for the previous model, it was not possible to test the interaction between the percentage of pairs and the group size because we did not have a complete crossover design. The random factors were the group identity and the repetition number.

NumberOfBurst ~ offset(log(RecordingDuration)) + GroupSize + PercentPair, random=GroupID, RepetitionNb

- Vocalization rate in bursts: We measured the overall vocalization rate in the bursts (for each burst, the vocalization rate was the total number of vocalizations produced by all individuals divided by the duration of this burst). We tested the influence of the group size and percentage of pair. We built a mixed linear model, and as for the previous model, it was not possible to test the interaction between the percentage of pairs and the group. The random factors were the group identity and the repetition number.

VocRateBurst ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

Vocalizations *rate autocorrelation*

We looked at the difference in the time lag of vocalization rate autocorrelation between different group compositions (0%, 50%, 100% of pairs). We detected the secondary maximum peak of each curve from each recording session (the first peak is at 0). For that we used the function 'find_peaks_cwt' from the 'signal' python library. We built the following model for each group size: AutocorrelationTimeLag ~ PercentPair random=GroupID, RepetitionNb.

Cross-correlation

We first build the following general model:

CrossCorr ~ GroupSize + PercentPair + Paired, random=GroupID, RepetitionNb, Bird1, Bird2.

Explanatory variables had different number of levels depending on group size: the distance between two birds was always 1 for the 2-bird groups, it was either 1 or 2 for the 4-bird groups, and it could be 1, 2, 3, or 4 for the 8-bird groups. Also, the percentage of pairs could only be tested in the 4-bird and 8-bird groups. We thus decided to split the dataset into three sets (one for each group size).

We built the following mixed linear models. The variable Paired was "yes" if the bird was paired with another bird in the group, and "no" otherwise. The random factors were the group identity, the repetition number, and the two birds' identities.

Group size=2: CrossCorr ~ Paired, random=GroupID, RepetitionNb, Bird1, Bird2.

Group size=4: We could not test the interaction between the Paired and Distance variables, because pairs were always at a distance of 1. It was also not possible to test the interaction between Paired and PercentPair because in groups with 100% of pairs, all birds were paired, and the opposite in groups of 0% pairs.

CrossCorr ~ PercentPair + Paired + Distance + PercentPair:Distance,
random=GroupID, RepetitionNb, Bird1, Bird2.

Group size=8: The model structure was the same as for the 4-bird groups model above.

CrossCorr ~ PercentPair + Paired + Distance + PercentPair:Distance,
random=GroupID, RepetitionNb, Bird1, Bird2.

We build a second model that included only the data from distance = 1:

CrossCorr ~ PercentPair * Paired + SameSexDyad + SameSexDyad:Paired,

random=GroupID, RepetitionNb, Bird1, Bird2

The variable SameSexDyad is 'yes' if the corresponding dyad is two females of two males, and 'no' if the corresponding dyad is one male and one female.

For the 8-bird groups, the interaction between PercentPair and Distance was significant. We focused on groups with 50% and 100% of pairs in order to test the interaction between PercentPair and Paired:

CrossCorr ~ PercentPair * Paired + Distance + PercentPair:Distance,

random=GroupID, RepetitionNb, Bird1, Bird2

Turn-taking transitions probability

We compared the mean transition probabilities between paired/unpaired and neighbours/non-neighbours dyads of birds. As all pairs were set up as neighbours, we had only three possibilities for each dyad of birds in a group with these parameters: UnPaired and NonNeighbour, UnPaired and Neighbour, Paired and Neighbour. As the intrinsic random probability of jumping from a caller i to a caller j depended on the group size (1/4 for 4-bird groups and 1/8 for 8-bird groups), we studied separately the different group sizes. We had not enough data to compute this metrics on the 2-bird groups. We used the following model for 4-bird and 8-bird groups:

MeanTransitionProba ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

with PairedNeighb a variable with the three possible levels: UnPaired and NonNeighbour, UnPaired and Neighbour, Paired and Neighbour.

Results

Effect of Group Size and Composition on Long-Term Vocal Dynamics

Individual vocalization rate and burst vocalization rate increase with group size

The group size had an effect on the individual vocalization rate: each bird vocalized more when in a larger group. The individual vocalization rate in 8-bird groups was 1.57 times [1.09;2.27] higher than the individual vocalization rate in 2-bird groups. The individual vocalization rate in 4-bird groups was intermediate between the 2-bird and 8-bird groups, but the differences between the 8-bird vs 4-bird and 4-bird vs 2-bird groups were not significant (Figure 2a, Table 2).

The number of bursts was higher in large groups than in small groups. The number of bursts was 1.27 times [1.03;1.55] higher in 4-bird groups than in 2-bird groups, and 1.47 times [1.22;1.80] higher in 8-bird groups than in 2-bird groups (Figure 2b, Table 3). The overall vocalization rate in bursts was also higher when the group size increased (Figure 2c, Table 3).

Individual vocalization rate decreases when the percentage of pairs increases in the group.

In 8-bird groups, we found that the percentage of pairs had an effect on the individual vocalization rate: the individual vocalization rate was lower in groups composed of 100% of pairs than in groups composed of unpaired birds only. In 8-bird groups, the individual vocalization rate was 1.35 times [1.01;1.82] lower in 100% pairs groups than in 0% pairs groups (Figure 3a, Table 2).

Waves of collective vocalizations have shorter cycles in groups only including unpaired birds

A peak at time T on the autocorrelation curve means that the vocalization rate activity presents a cycle of duration T. Groups' compositions (0%, 50%, 100% of pairs) were compared at different time lag T (Figure 3b for 8-bird groups, Table 4).

In 8-bird groups, the vocalization rate autocorrelation in 0% pairs groups presented a peak at around 36min +/- 13min (mean +/- sd). In 50% pairs groups, the peak was around 46 min +/- 14 min, and in 100% pairs groups the peak was around 61min +/- 15min. The time lag tended to be significant between 0% and 100% pairs groups (Figure 3b, Table 4), suggesting that 0% pairs groups had shorter cycles of collective vocalizations than 50% and 100% pairs groups.

In 4-bird groups, the vocalization rate autocorrelation in 0% pairs groups presented a peak at around 47min +/- 15min (mean +/- sd). In 50% pairs groups, the peak was around 58 min +/- 13 min, and in 100% pairs groups the peak was around 60min +/- 11min. We found no significant difference between groups (Figure 3b, Table 4).

Effect of Pair-Bonds and spatial proximity on Short-Term Vocal Dynamics

Vocal synchrony is higher within pairs and decreases with the distance between individuals

We compared cross-correlation between paired/unpaired and neighbour/non-neighbour birds. Two birds showed a high cross-correlation value if they usually vocalized (or stayed silent) closely in time (within 500ms) (i.e "vocal synchrony"). The full model showed no effect of group size or percentage of pairs on dyads' cross-correlation (Table 5). We then split the dataset by group size (see Methods). First, in 2-bird groups, paired and unpaired birds did not differ in cross-correlation (Table 5, Figure 4a). In 4-bird groups, the cross-correlation of a dyad was significantly higher if the

birds were paired, and decreased with the distance (Figure 4b, Table 5). There was no effect of the percentage of pairs in 4-bird groups. Finally, in 8-bird groups, the cross-correlation also decreased with the distance (Figure 4c). At distance = 1, the cross-correlation between two paired birds was higher than between two unpaired birds (unpaired female/male dyads or same sex unpaired dyads, Supplementary Figure 3, Table 5). The cross-correlation between two paired birds was lower in groups composed of 50% of pairs than in groups composed of 100% of pairs (Table 5, Figure 4d). The detailed results on the cross-correlation for each group of 8 birds with 100% of pairs are presented in Supplementary Figure 4.

Turn-taking transitions probability is higher within pairs, and is higher between neighbours.

We compared the mean transition probabilities between two birds when paired/unpaired and neighbour/non-neighbour. Two birds showed a high mean transition probability if they usually vocalized one after the other. Figure 5 shows the distributions of mean transition probabilities between two birds (paired/unpaired and neighbour/non-neighbour). For both group sizes (4 birds and 8 birds), the mean transition probabilities were higher for UnPaired – Neighbour birds than for UnPaired – NonNeighbour, and even higher for Paired – Neighbour birds. In other words, two paired birds were more likely to vocalize one after the other than two unpaired birds. Within the unpaired birds, two neighbour birds were more likely to vocalize one after the other than two non-neighbour birds. The statistical results are presented in Table 6.

Discussion

In this article, we showed that the organization of group vocal activity reveals some aspects of group structure (such as group size and composition) and group acoustic network. On a long-term scale (several minutes to an hour), zebra finches groups synchronize their general vocal activity with waves of collective vocalizations that increase with group size and whose cycles' duration increases with the percentage of pairs in the group. We also showed that the group influences individual vocal activity, with individual vocalization rates increasing with group size and decreasing with the percentage of pairs in the group. On a short-term scale (a few seconds), acoustic interactions are shaped by pair-bonds and distance, as birds preferentially vocalize at the same time (synchrony) or directly after (turn-taking) their partner when it is present, and the nearest neighbour when the partner is not available.

Our setup allowed automatically detecting and extracting vocalizations from hours of passive recording depicting a 'basal' social situation. Our system is able to extract a lot of individual vocalizations (a bit less than 2M for all experiments combined) with individual tagging. We retrieved a bimodal distribution of duration (well predicted by a sum of two Gaussian) that may relate to the two main types of calls uttered in that context: tets/stacks and distance calls (as well as song syllables).

First, on a long-term scale (several minutes to an hour), we saw that large groups have a higher burst rate, and a higher vocal activity within these bursts. This bursting activity can be compared to other waves of collective behaviour (G. Fernandez, Capurro, & Reboreda, 2003; Pays et al., 2007). For example, in Defassa waterbuck, (*Kobus ellipsiprymnus defassa*), waves of collective vigilance against predators emerge from group members synchronizing scanning and non-scanning bouts and are triggered by allelomimetic effects, i.e. each individual copying its

neighbour's behaviour (Pays et al., 2007). Focusing on a short-term scale (a few seconds), we saw that neighbouring birds are more likely to vocalize together within a short time window and one after the other. Some individuals could initiate bursts and then neighbours would vocalize as well, triggering waves by an allelomimetic effect. With this hypothesis, the higher bursting activity observed in large groups would be the consequence of the observed increase of the individual vocalization rate. This could be due to a driving effect, because in larger groups there are more individuals to interact with. In killer whales (*Orcinus orca*), an increase of the production of some vocalization types has been described during socializing and beach-rubbing activities, also corresponding to periods when the group size increases (Ford, 1989). In savanna elephants (*Loxodonta africana*), it has been shown that the group vocal activity increases when the group size increases (Payne, Thompson, & Kramer, 2003).

One alternative hypothesis to the allelomimetic effect would be that group members exchange information during group vocal interactions. In black-capped chickadees (*Poecile atricapillus*), dawn choruses can be seen as an interactive communication network. In a recent study, males' dawn chorus singing behaviour was examined by determining the level of song frequency matching between neighbours: male black-capped chickadees were observed having a high level of matching with their neighbours and they also match other individuals simultaneously and sequentially (Foote, Fitzsimmons, Mennill, & Ratcliffe, 2010).

If allelomimetic effects structure group vocal activity, the bursting activity of the group would correlate with the mean individual vocalization rate in the group. To test this prediction, recordings on more groups are needed. On the other hand, if group vocal activity is an information exchange, the group would display strategies to maintain communication efficacy in response to noise. To test this prediction, recordings of groups subjected to background noise playbacks and measures of the response of the group vocal dynamics are needed.

As highlighted above, in our study two birds at short distance are more likely to vocalize together

(or stay silent together) within a short time window, but this is even more likely if they are paired. In 4-bird groups, neighbour birds were always one male and one female, thus we cannot conclude if the difference of cross-correlation observed is due to the distance or to the intersexual nature of the dyad. Also, we chose to put pairs in neighbour cages to avoid the stress of separation. This is why we could not test whether pairs would show the same behaviour when at longer distance. However the results show that unpaired birds being located at short distance are less likely to vocalize together within a short time window than paired birds at this same distance. In many taxonomic groups, a likely candidate for directing signals to a specific individual is relative signal timing, that is, close temporal association (McGregor, Otter, & Peake, 2000; Naguib, 1999). In African elephant (*Loxodonta africana)*, it has been shown that females are more likely to produce rumbles shortly after rumbles from other group members. Also, an affiliative relationship with a caller has a strong influence on the probability of a rumble response, whereas the relative dominance rank and reproductive state has no effect (Soltis, Leong, & Savage, 2005). Another study showed that in Squirrel Monkeys (*Saimiri Sciureus*), mutually preferred partners exchange chucks more often and with shorter latencies of response than other individuals (Biben, Symmes, & Masataka, 1986). This result is also consistent with recent studies on zebra finches groups: Ter Maat et al. (2014) show that paired males and females recorded in groups communicate using bilateral stack calling, Gill et al. (2015) show that zebra finches calls occur non-randomly in vocal interactions. Also, Stowell et al. (2016) developed a model that reflects fine details of zebra finches vocal interactions networks, and that especially models the timing and influence strengths between individuals in a group. They showed that within-pair vocal interactions were dominant in the group calling network.

The analysis of the transition probabilities between callers also shows that two birds at short distance were more likely to vocalize one after the other. This result on the preferred turn-taking is even stronger if birds are paired. Studies on mammal and bird species with different levels of social coordination show that the social structure of the species relate to different dynamics in their

vocal interactions. A recent study shows that in the European starling, the direct and general social context, as well as the individual history, and the internal state of the caller can influence the dynamics of vocalizations in time and structure (Henry, Craig, Lemasson, & Hausberger, 2015). In our study, we set up the cages in a way that each bird was able to see the whole group, but it was perhaps less easy for a bird to get the visual signals from a bird located far away. If neighbour birds could exchange more visual signals, they might be more likely to answer each other's vocalizations. In human conversation, changes in gazing is one of the signs used to guide conversational turn-taking (Gérard, 1987; Hauser, 1992).

The vocalization rate was lower for the 8-bird groups containing only paired birds than for 8-bird groups containing only unpaired birds. This is consistent with a previous study (Elie et al., 2011) that described zebra finch groups' communal vocalizations (without identification of the callers). Birds involved in a pair-bond could answer preferentially to their partner and less to other members of the group. On the contrary, unpaired birds would have no initial preference and would interact with more birds in the group ("driving effect" suggested above).

Additionally, the autocorrelation analysis showed that the vocal cycling pattern differed with group composition. Groups of eight unpaired birds have shorter cycles that peak around 36min, with a more consistently cycling activity. This is consistent with the previous study from Elie et al. (2011) showing that groups of zebra finches comprising less pairs had shorter vocal cycles.

In larger groups, pairs were more likely to be vocally synchronized in groups containing only pairs than in groups also containing unpaired birds. This could be explained by the fact that, in groups containing unpaired birds, more birds are available for interaction, whereas in groups containing only pairs, each bird may be busy interacting with its own partner as suggested above (Biben et al., 1986; Soltis et al., 2005).

This last result is not observed in intermediate group sizes. One reason could be that 4-bird groups with 50% of pairs are actually composed of one unique pair, one unpaired male and one unpaired female. The number of unpaired birds potentially available is thus smaller than in 8-bird groups of 50% of pairs (composed by two pairs, two unpaired females and two unpaired males).
For this same metric, groups of two birds showed no difference between paired or unpaired birds. In these dyads, birds had only one other individual to interact with. Because zebra finches are gregarious birds that use vocal interactions to find and keep social contact (Perez, Fernandez, Griffith, Vignal, & Soula, 2015; Zann, 1996), they might interact with whoever is available when placed in dyads.

In this study we decided to keep all vocalizations types together because among all vocalizations types that zebra finches can produce, in the conditions of our experiment (non-breeding birds and cages at short distances) only three of them were produced: tets, distance calls and songs with a clear bimodal distribution of durations. Separating vocalizations according to duration did not change our results. However it would probably be interesting to study the vocal dynamics by separating the different vocalization types, because the dynamic of vocal exchange could change according to call type, as suggested by (Gill et al., 2015).

Also, constraining the birds in one location can be seen as a limitation. Using this protocol we are able to study the acoustic network by constraining the position (in addition to be able to tag individual vocalization more easily). Of course, these position constraints will affect calling dynamics and cannot describe neither situations like group gathering in a social tree, nor interaction contexts like agonistic or physical affiliative behaviours, foraging, etc. So, constraining the spatial position of individuals may have direct and indirect effects on vocal dynamics (Elie et al., 2011). A recent study used devices mounted on the birds to assign vocalizations in bird groups (Gill et al., 2015). This method allows for the study of free-ranging networks of birds in different contexts (agonistic and affiliative behaviours, foraging, and different breeding conditions), and has

578 the advantage of investigating the calling behaviour of birds behaving freely in a social group.
579 However, it does not give the spatial position of each bird, which can also have an impact on the
580 vocal dynamics. New technologies need to be explored to be able to control for these different
581 aspects at the same time.

582 Here we show that zebra finches groups synchronize their general vocal activity with waves of
583 collective vocalizations, which depend on group size and group composition. Furthermore, at a
584 finer level we show that the group vocal activity is structured by the presence of pairs in the group.
585 Thus we demonstrate that from the acoustic network measured at the individual level we can
586 extract information about the social network.

587

588

589 **Figures legends**

590

591 **Figure 1: Schematic of the protocol**.

592 Groups of 2, 4, and 8 birds were built, with one bird per cage and one microphone on the top of
593 each cage. Pair mates were put in neighbour cages to reduce stress (distance=1).

594

595 **Figure 2: Impact of group size on long-term vocal dynamics** (a) Effect of group size on
596 individual vocalization rates. (b) Effect of group size on burst rate (number of bursts per hour). (c)
597 Effect of group size on vocalization rate in bursts. Boxes are median, first and third quartiles (Q1
598 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value
599 and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of
600 the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR
601 are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the
602 low end. *: P<0.05, **:P<0.001, ***:P<0.0001

603

604 **Figure 3: Impact of the percentage of pairs on the long-term vocal dynamics**

605 (a) Effect of group composition (0%, 50%, and 100% of pairs in the group) on individual
606 vocalization rates in 8-bird groups. (b) Autocorrelation of the number of vocalizations (time
607 step=3min, overlap=1.5min). Boxes are median, first and third quartiles (Q1 and Q3 respectively).
608 The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile
609 Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 -
610 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the
611 high end, and those below Q1 - 1.5 IQR are plotted separately on the low end.. *: P<0.05

612

613 **Figure 4: Vocal cross-correlation between two birds**

(a) Effect of pair-bonds on cross-correlation in 2-bird groups, (b) Effect of pair-bonds and distance (1, 2) on cross-correlation in 4-bird groups, (c) Effect of pair-bonds and distance (1, 2, 3, 4) on cross-correlation in 8-bird groups, (d) Effect of pair-bonds and group composition (% of pairs) on cross-correlation in 8-bird groups. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end. *: P<0.05, **:P<0.001, ***:P<0.0001.

Figure 5: Vocal transition probabilities between two birds

Distribution of the average vocal transition probability in (a) 4-bird groups, (b) 8-bird groups. *: P<0.05, **:P<0.001, ***:P<0.0001.

Supplementary Figure 1: **Detection and attribution of calls to individuals.** We tested the detection and attribution of vocalizations to individuals in the three possible positions of a bird in the room (i.e. one angle and two edges, the remaining cages being symmetrical). We put one bird in a cage and recorded it, and repeated the recording in the three possible positions. We had a success rate of 100% over 240 calls produced (containing tets/stacks and distance calls). The figure provides the sonograms (in green/yellow) and oscillograms (in red) from the 8 microphones for two examples of vocalizations.

Supplementary Figure 2: **Histograms of all female and male vocalizations' durations of this study.** (a) Female vocalizations' durations, (b) Male vocalizations' duration. Tets/stacks and distance calls were detected (resp. first and second peaks) for each sex. Songs were also automatically detected but split so each syllable was considered as a vocalization.

Supplementary Figure 3: **Vocal cross-correlation between two birds at distance 1 in 8-bird groups.**

Effect of sex and pair-bond on cross-correlation at distance 1 in 8-bird groups. Boxes are median, first and third quartiles (Q1 and Q3 respectively). The upper whisker is located at the *smaller* of the maximum x value and Q3 + 1.5 Inter Quartile Range (IQR), whereas the lower whisker is located at the *larger* of the smallest x value and Q1 - 1.5 IQR. Individual points more extreme in value than Q3 + 1.5 IQR are plotted separately at the high end, and those below Q1 - 1.5 IQR are plotted separately on the low end. NS: non-significant, ***: P<0.0001.

Supplementary Figure 4: **Acoustic networks for each group in 8-bird groups with 100% of pairs.** Nodes are individuals (P_i states for individual in pair i). Edges thickness is an affine function of the average vocal cross-correlation on the four recording days for each dyad.

Tables legends

Table 1: Number of groups for each social composition

For each group size and composition, we give the number of groups recorded (i.e. groups with different birds, X= impossible group social composition). In brackets is the number of recording days for each group. The third element is the total number of hours recorded for each combination.

Table 2: Statistical results of the impact of group composition on individual vocal activity.

The full model is presented. Then each group size is analyzed separately and each model is provided. NVocN stands for the number of vocalizations in groups of N birds.

R^2c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

from the summary of the model.

Table 3: Statistical results of the impact of group composition on bursts activity

R^2c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results from the summary of the model.

Table 4: Statistical results of the impact of group composition on the autocorrelation of the number of vocalizations over time

R^2c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results from the summary of the model.

Table 5: Statistical results of the impact of group composition on vocal cross-correlation

The full model is presented. Then each group size is analyzed separately and each model is provided. CrossCorrN stands for the cross-correlation values in groups of N birds.

R^2c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results from the summary of the model.

Table 6: Statistical results of the impact of group composition on vocal mean transitions probabilities.

Groups with four and eight birds are analyzed separately, and each model is provided. MeanTransitionProbaN stands for the mean transition probability values in groups of N birds.

R^2c value, which represents the conditional coefficient of determination of the model, is indicated for each model ('r.squaredGLMM' function of 'MuMIn' R package). The table presents the results

692 from the summary of the model.

693

694

695 **Supplementary Table 1:** Results on the estimation of vocalization duration parameters.

696 We used a sum of two Gaussians and the fit was made on the duration histogram (time

697 step=10ms on 0-1s interval) with the least square method.

698

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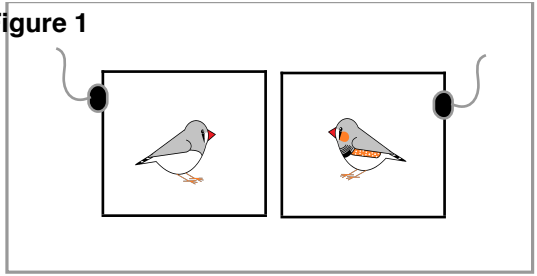
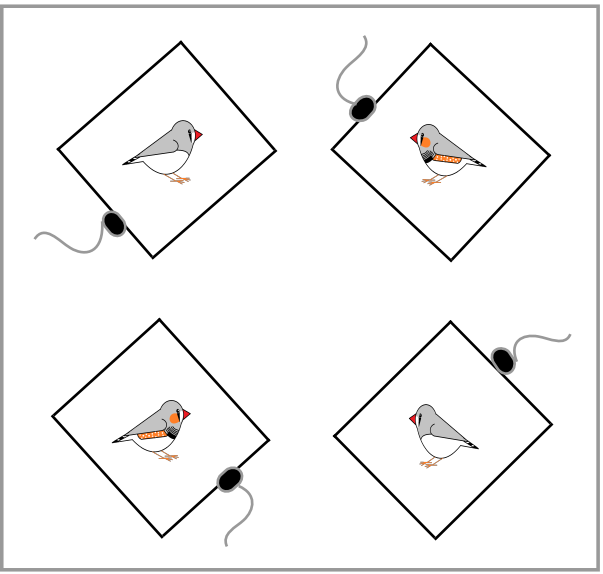
Acknowledgments

This work was supported by an ANR grant (French Agence Nationale de la Recherche, project ‘Acoustic Partnership’) and an IUF grant (Institut Universitaire de France) to C.V., a joint NSF/ANR e CRCNS grant ‘AuComSi’ for M.S.A.F. and H.A.S.. We are grateful to Colette Bouchut and Nicolas Boyer for their help at the ENES lab. We also thank Caroline Lothe for her help at Beagle Lab. We thank Ingrid Boucaud for the zebra finch drawing.

Figure 1



Group size = 2



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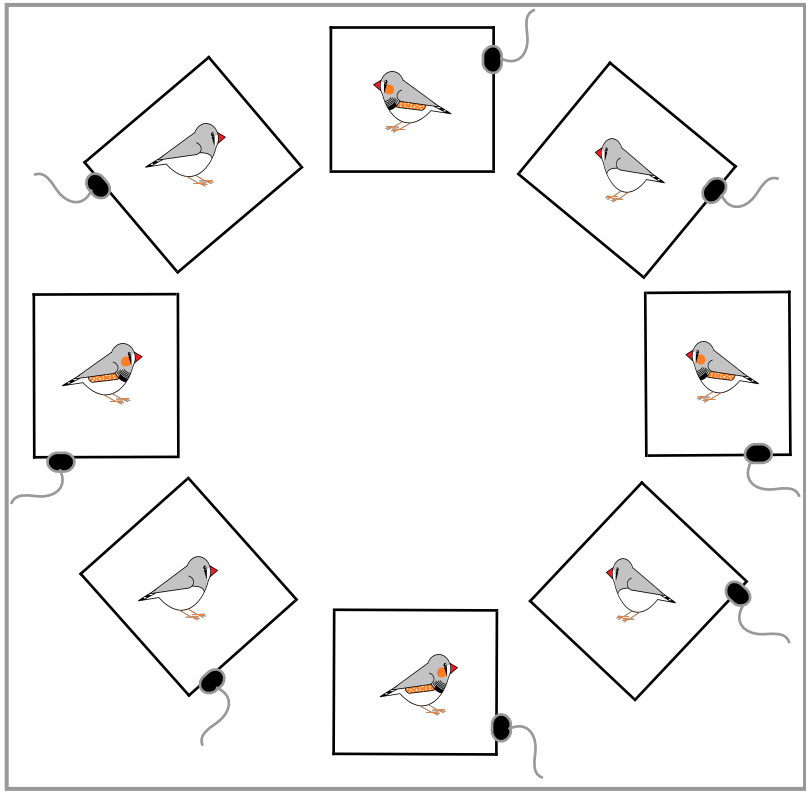


Group size = 8

Figure 2

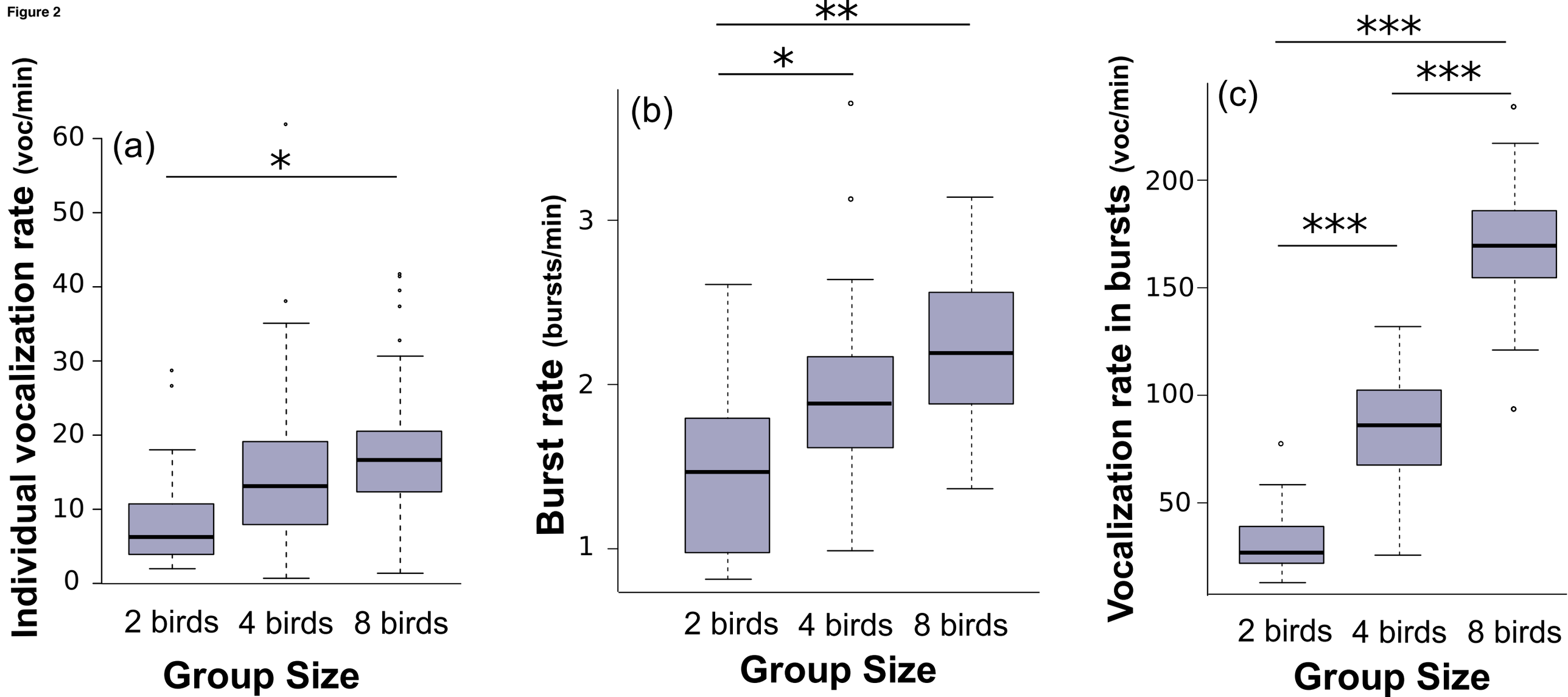

(a)
Individual vocalization rate (voc/min)
0
10
20
30
40
50
60
*
2 birds
4 birds
8 birds
Group Size
(b)
Burst rate (bursts/min)
1
2
3
*
**
2 birds
4 birds
8 birds
Group Size
(c)
Vocalization rate in bursts (voc/min)
50
100
150
200
***
***
***
2 birds
4 birds
8 birds
Group Size

Figure 3

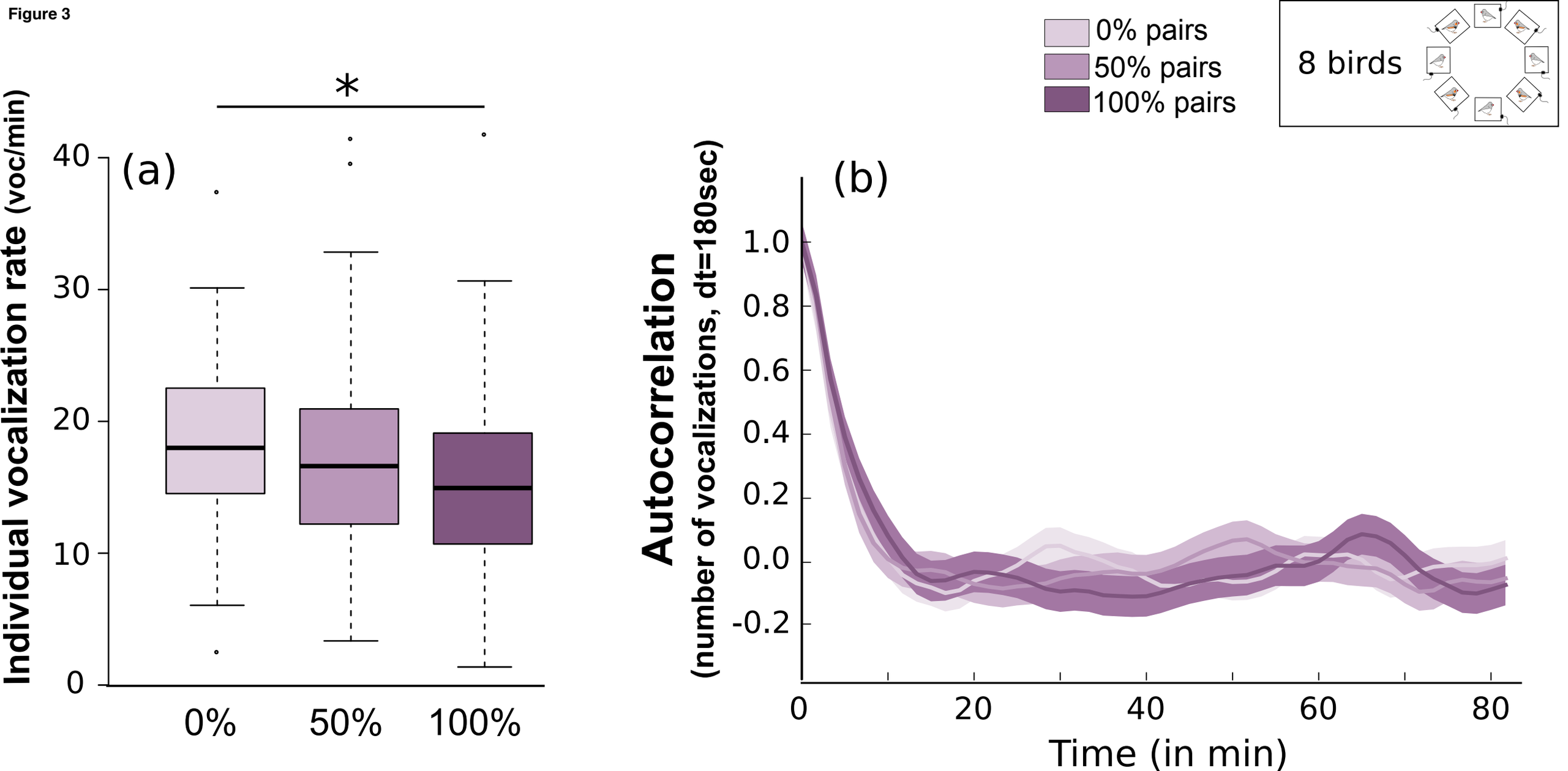

0% pairs
50% pairs
100% pairs
8 birds
(a)
*
Individual vocalization rate (voc/min)
40
30
20
10
0
0%
50%
100%
(b)
Autocorrelation
(number of vocalizations, dt=180sec)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0
20
40
60
80
Time (in min)

Figure 4

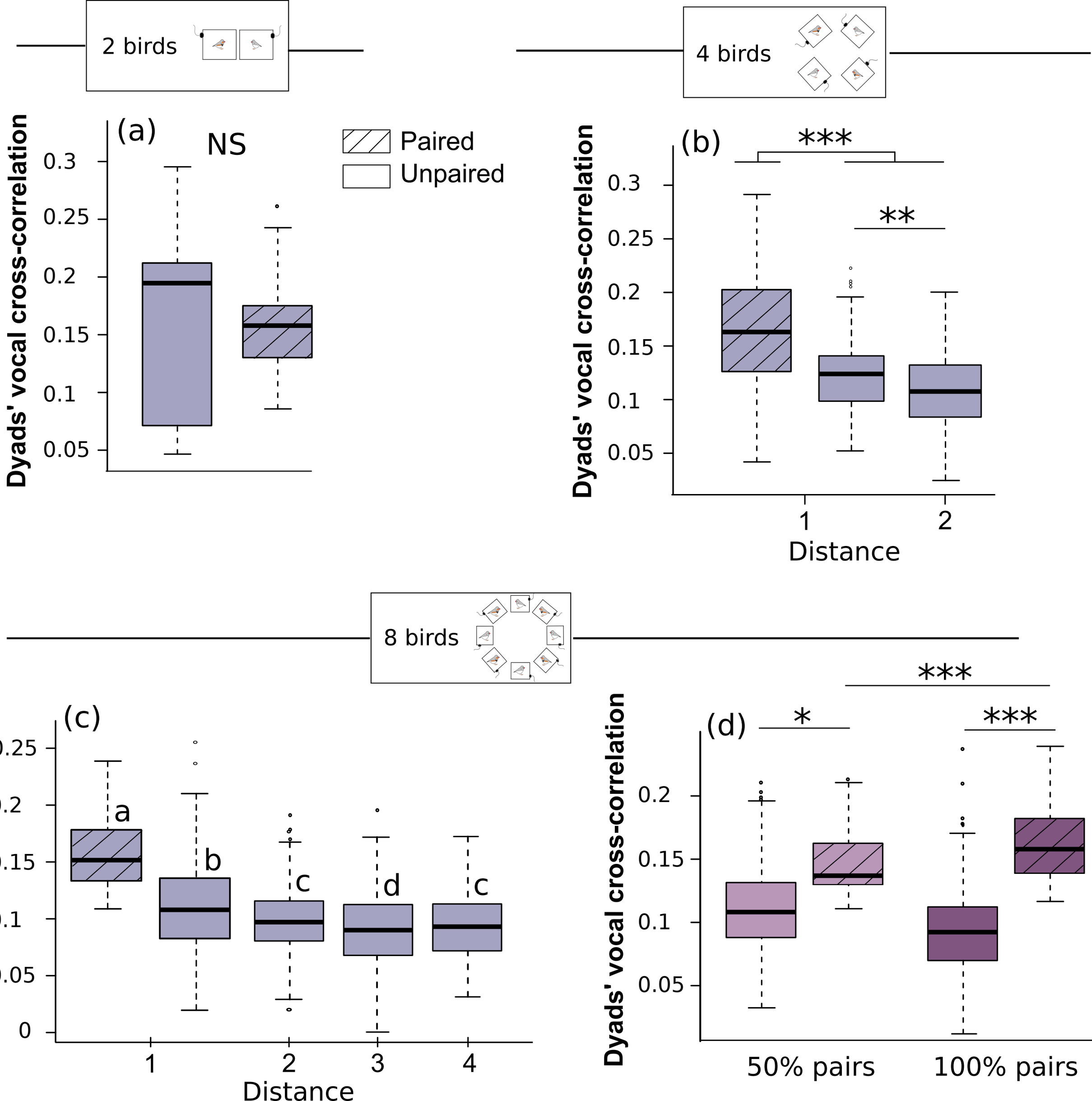
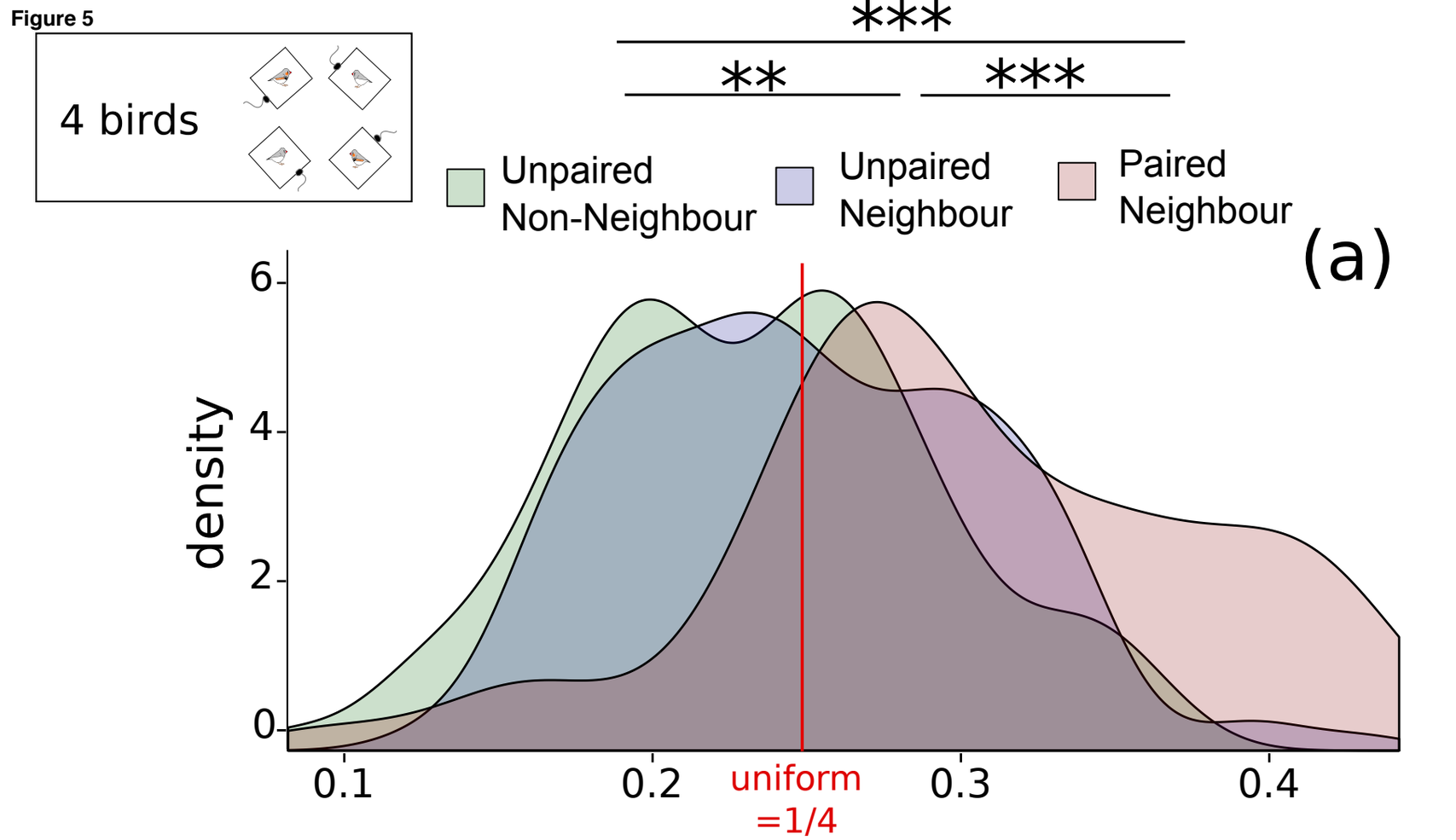
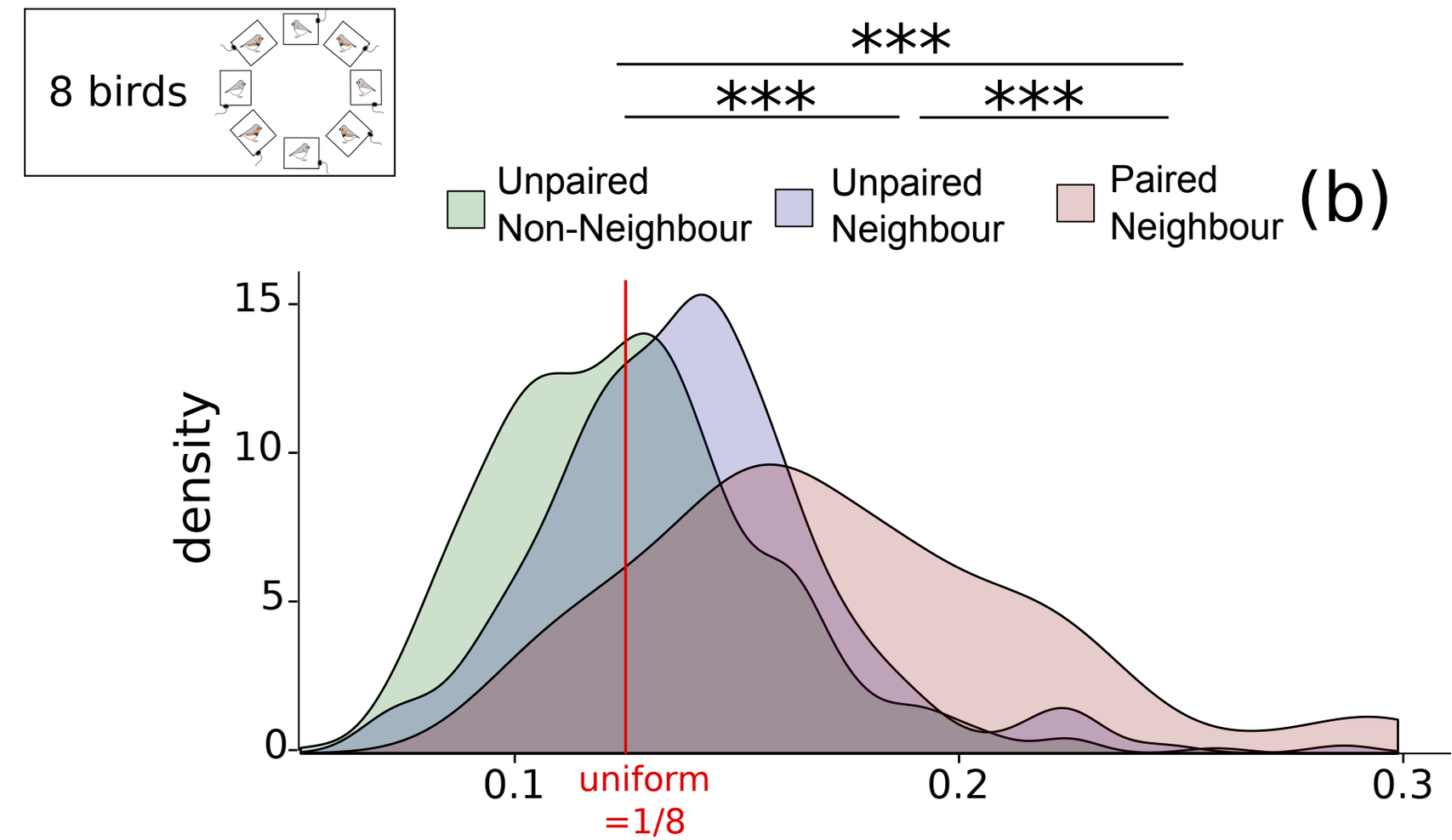

2 birds
4 birds
8 birds
(a)
NS
Paired
Unpaired
Dyads' vocal cross-correlation
0.3
0.25
0.2
0.15
0.1
0.05
(b)
***
**
1
2
Distance
(c)
a
b
c
d
c
0.25
0.2
0.15
0.1
0.05
0
1
2
3
4
Distance
(d)
*
***
***
0.2
0.15
0.1
0.05
50% pairs
100% pairs

Figure 5





Average of transition probabilities between 2 birds

Ethical Note

Experiments were performed under the authorization no. 42-218-0901-38 SV 09 (ENES Laboratory, Direction Départementale des Services Vétérinaires de la Loire) and were in agreement with French and European legislation regarding experiments on animals.

Table 1

group size	0% paired	50% paired	100% paired
2	6 (1) -36h	X	4 (2) + 7(1) - 89h
4	3 (4) - 46h	3 (4) - 42h	3 (4) - 86h
8	3 (4) - 45h	3 (4) - 36h	3 (4) - 46h

Table 2

NVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair), random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.10291	0.3208
BirdID : GroupID	0.06534	0.2556
RepetitionNB	0.0263	0.1622
Residual	0.9343	0.9666

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.3475	0.1887	12.436	<0.0001
BirdSexM	-0.2145	0.1671	-1.284	0.1991
GroupSize4	0.1904	0.1741	1.094	0.2742
GroupSize8	0.4565	0.1856	2.46	0.0139
PercentPair50	-0.0538	0.2071	-0.26	0.7951
PercentPair100	-0.2098	0.1556	-1.349	0.1774
BirdSexM : GroupSize4	0.4405	0.1715	2.568	0.0102
BirdSexM : GroupSize8	0.2524	0.1656	1.524	0.1275
BirdSexM : PercentPair50	-0.0016	0.1460	-0.011	0.991
BirdSexM : PercentPair100	0.0810	0.1243	0.652	0.5145

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.1904	0.1741	1.094	0.517
GroupSize8 - GroupSize2	0.4565	0.1856	2.46	0.0368
GroupSize8 - GroupSize4	0.2662	0.1604	1.66	0.22

NVoc2 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05774	0.2403
Residual	1.10656	1.0519

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	1.93702	0.25458	7.609	<0.0001
BirdSexM	-0.06731	0.35642	-0.189	0.85
PercentPair100	0.29708	0.31197	0.952	0.341
BirdSexM : PercentPair100	-0.22783	0.43006	-0.53	0.596

NVoc4 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05626	0.2372
GroupID	0.16096	0.4012
RepetitionNB	0.04658	0.2158
Residual	0.92949	0.9641

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.73556	0.29264	9.348	<0.0001
BirdSexM	0.07808	0.17659	0.442	0.658
PercentPair50	-0.30736	0.38237	-0.804	0.421
PercentPair100	-0.41704	0.31717	-1.315	0.189
BirdSexM : PercentPair50	0.29995	0.24969	1.201	0.23
BirdSexM : PercentPair100	0.22832	0.21404	1.067	0.286

NVoc8 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, randon BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
BirdID	0.06748	0.2598
GroupID	0.01339	0.1157
RepetitionNB	0.01741	0.1319
Residual	0.91694	0.9576

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.8465	0.1334	21.329	<0.0001
BirdSexM	0.0618	0.1281	0.483	0.6293
PercentPair50	-0.0706	0.1624	-0.435	0.6635
PercentPair100	-0.2993	0.1526	-1.961	0.0499
BirdSexM : PercentPair50	-0.1042	0.1823	-0.571	0.5677
BirdSexM : PercentPair100	0.0981	0.1718	0.571	0.5678

n=GroupID,

Table 3

NumberOfBursts ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.00	0.00
RepetitionNB	0.001042	0.03228

Fixed effects:

	Estimate	Std. Error	zvalue	pvalue
(Intercept)	-3.6733	0.1169	-31.409	<0.0001
GroupSize4	0.2460	0.1096	2.243	0.0248
GroupSize8	0.3916	0.1232	3.177	0.0014
PercentPair50	0.0215	0.1023	0.21	0.8335
PercentPair100	-0.0437	0.0828	-0.528	0.5971

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.24605	0.10969	2.243	0.06196
GroupSize8 - GroupSize2	0.39161	0.12325	3.177	0.00411
GroupSize8 - GroupSize4	0.14556	0.08293	1.755	0.17993

VocalizationRateBurst ~ GroupSize + PercentPair, random=GroupID, RepetitionNb

R2c = 0.89

Random effects:

Groups Name	Variance	Std.Dev.
GroupID (intercept)	230.1	15.17
RepetitionNB (intercept)	171.3	13.09
Residual	326.6	18.07

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	50.083	9.111	10.37	5.497	2.31 e-04
GroupSize4	41.308	6.538	47.1	6.318	<0.0001
GroupSize8	121.479	7.248	40.89	16.76	<0.0001
PercentPair50	-2.459	8.458	31	-0.291	0.7731
PercentPair100	-6.119	6.189	40.05	-0.989	0.3287

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	41.308	6.538	6.318	<0.0001
GroupSize8 - GroupSize2	121.479	7.248	16.76	<0.0001
GroupSize8 - GroupSize4	80.171	6.567	12.208	<0.0001

NbVoc ~ offset(log(RecordingDuration)) + BirdSex * (GroupSize + PercentPair), random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.10291	0.3208
BirdID : GroupID	0.06534	0.2556
RepetitionNB	0.0263	0.1622
Residual	0.9343	0.9666

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.3475	0.1887	12.436	<0.0001
BirdSexM	-0.2145	0.1671	-1.284	0.1991
GroupSize4	0.1904	0.1741	1.094	0.2742
GroupSize8	0.4565	0.1856	2.46	0.0139
PercentPair50	-0.0538	0.2071	-0.26	0.7951
PercentPair100	-0.2098	0.1556	-1.349	0.1774
BirdSexM : GroupSize4	0.4405	0.1715	2.568	0.0102
BirdSexM : GroupSize8	0.2524	0.1656	1.524	0.1275
BirdSexM : PercentPair50	-0.0016	0.1460	-0.011	0.991
BirdSexM : PercentPair100	0.0810	0.1243	0.652	0.5145

Pairwise comparisons (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
GroupSize4 - GroupSize2	0.1904	0.1741	1.094	0.517
GroupSize8 - GroupSize2	0.4565	0.1856	2.46	0.0368
GroupSize8 - GroupSize4	0.2662	0.1604	1.66	0.22

NbVoc2 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05774	0.2403
Residual	1.10656	1.0519

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	1.93702	0.25458	7.609	<0.0001
BirdSexM	-0.06731	0.35642	-0.189	0.85
PercentPair100	0.29708	0.31197	0.952	0.341
BirdSexM : PercentPair100	-0.22783	0.43006	-0.53	0.596

NbVoc4 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID/BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
GroupID/BirdID	0.05626	0.2372
GroupID	0.16096	0.4012
RepetitionNB	0.04658	0.2158
Residual	0.92949	0.9641

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.73556	0.29264	9.348	<0.0001
BirdSexM	0.07808	0.17659	0.442	0.658
PercentPair50	-0.30736	0.38237	-0.804	0.421
PercentPair100	-0.41704	0.31717	-1.315	0.189
BirdSexM : PercentPair50	0.29995	0.24969	1.201	0.23
BirdSexM : PercentPair100	0.22832	0.21404	1.067	0.286

NbVoc8 ~ offset(log(RecordingDuration)) + BirdSex * PercentPair, random=GroupID, BirdID, RepetitionNb

Random effects:

Groups Name	Variance	Std.Dev.
BirdID	0.06748	0.2598
GroupID	0.01339	0.1157
RepetitionNB	0.01741	0.1319
Residual	0.91694	0.9576

Fixed effects:

	Estimate	Std. Error	tvalue	pvalue
(Intercept)	2.8465	0.1334	21.329	<0.0001
BirdSexM	0.0618	0.1281	0.483	0.6293
PercentPair50	-0.0706	0.1624	-0.435	0.6635
PercentPair100	-0.2993	0.1526	-1.961	0.0499
BirdSexM : PercentPair50	-0.1042	0.1823	-0.571	0.5677
BirdSexM : PercentPair100	0.0981	0.1718	0.571	0.5678

Table 4

8 birds: Autocorrelation ~ PercentPair, random=GroupID

R2c = 0.25

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	24.97	4.997
Residual	184.78	13.594

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	42.1250	4.8704	5.9960	8.649	1.32.e-03
PercentPair50	0.9739	6.9954	6.3350	0.139	0.8936
PercentPair100	13.1045	6.6521	6.7760	1.970	0.0908

4 birds: Autocorrelation ~ PercentPair

R2c = 0.02

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	52.125	3.888	13.408	13.408	<0.0001
PercentPair50	3.500	5.498	0.637	0.637	0.528
PercentPair100	5.250	4.918	1.068	1.068	0.292

Table 5

CrossCorr ~ GroupSize + PercentPair + Paired, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.79

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.482e-02	0.121738
Bird1ID	3.734e-03	0.061110
Bird2ID	3.124e-03	0.055896
RepetitionNB	5.266e-05	0.007257
Residual	6.564e-03	0.081021

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3488	0.0511	35.3	-26.389	<0.0001
GroupSize4	0.0201	0.0539	27	0.374	0.708
GroupSize8	-0.0067	0.0596	24.8	-0.114	0.916
PercentPair50	-0.0621	0.0681	19.5	-0.913	0.381
PercentPair100	-0.0841	0.0500	24.4	-1.681	0.111
PairedYes	0.1892	0.0101	1109	18.564	<0.0001

CrossCorr2 ~ Paired, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.87

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.671e-04	0.0129
Bird1ID	0.0195	0.1398
Bird2ID	0.0113	0.1065
RepetitionNB	0.0000	0.0000
Residual	0.0047	0.0686

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.2680	0.0669	11.963	-18.934	<0.0001
Paired	0.0014	0.0403	1.781	0.035	0.976

CrossCorr4 ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.70

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0035	0.0593
Bird1ID	0.0051	0.0719
Bird2ID	0.0043	0.0660
RepetitionNB	0.0000	0.0000
Residual	0.0075	0.0871

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3184	0.0487	10.46	-27.075	<0.0001
PercentPair50	-0.0476	0.0696	10.91	-0.684	0.5081
PercentPair100	-0.0496	0.0589	12.38	-0.842	0.4156
PairedYes	0.1565	0.0244	139.36	6.398	<0.0001
Dist2	-0.0653	0.0240	210.69	-2.715	0.0071
PercentPair50:Dist2	0.0246	0.0341	209.11	0.723	0.4707
PercentPair100:Dist2	0.0512	0.0308	202.26	1.662	0.0980

*Pairwise comparisons Paired * Dist (Tukey adjustment):*

Contrast	Estimate	SE	df	tratio	pvalue
PairedNo Dist1 - PairedYes Dist1	-0.1565	0.0252	138.15	-6.208	<0.0001
PairedNo Dist1 - PairedNo Dist2	0.0400	0.0132	208.30	3.030	0.0145
PairedYes Dist1 - PairedNo Dist2	0.1965	0.0259	143.43	7.580	<0.0001

CrossCorr8 ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.74

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.344e-03	0.0366
Bird1ID	2.633e-03	0.0513
Bird2ID	2.182e-03	0.0467
RepetitionNB	4.229e-05	0.0065
Residual	2.774e-03	0.0526

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.3003	0.0268	7.4	-48.503	<0.0001
PercentPair50	0.0469	0.0378	7.4	1.242	0.2524

PercentPair100	0.0327	0.0358	7.7	0.913	0.3885
PairedYes	0.1042	0.0120	839.1	8.687	<0.0001
Dist2	0.0236	0.0082	930.3	-2.868	0.0042
Dist3	-0.0679	0.0088	961.6	-7.706	<0.0001
Dist4	-0.0359	0.0106	949.8	-3.384	0.0007
PercentPair50:Dist2	-0.0202	0.0121	928.9	-1.671	0.0951
PercentPair100:Dist2	-0.0144	0.0121	922.4	-1.186	0.2360
PercentPair50:Dist3	0.0208	0.0129	960.8	1.602	0.1095
PercentPair100:Dist3	0.0074	0.0131	958.1	0.566	0.5713
PercentPair50:Dist4	-0.0143	0.0155	948.6	-0.927	0.3540
PercentPair100:Dist4	-0.0245	0.0152	942.3	-1.608	0.1081

Pairwise comparisons Dist (Tukey adjustment):

Contrast	Estimate	SE	zvalue	pvalue
Dist2-Dist1	-0.0213	0.0077	-2.767	0.0285
Dist3-Dist1	-0.0615	0.0082	-7.453	<0.0001
Dist4-Dist1	-0.0324	0.0099	-3.262	0.0056
Dist3-Dist2	-0.0401	0.0074	-5.374	<0.0001
Dist4-Dist2	-0.0110	0.0092	-1.197	0.6252
Dist4-Dist3	0.0290	0.0089	3.262	0.0059

CrossCorr8_Dist1 ~ PercentPair + Paired + SameSexDyad, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.72

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	1.114e-03	0.0333
Bird1ID	2.426e-03	0.0492
Bird2ID	1.933e-03	0.0439
RepetitionNB	3.491e-05	0.0059
Residual	2.744e-03	0.0523

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.2708	0.0246	7.2	-51.575	<0.0001
PercentPair50	0.0339	0.0346	7	0.979	0.360
PercentPair100	0.0090	0.0325	7.1	0.279	0.788
PairedYes	0.1427	0.0097	793.2	14.628	<0.0001
SameSexDyadYes	0.0016	0.0035	882.7	0.477	0.634

*Pairwise comparisons Paired*SameSexDyad(Tukey adjustment):*

Contrast	Estimate	SE	df	t ratio	pvalue
Unpaired FM - Unpaired FF/MM	-0.0016	0.0035	888.17	-0.477	0.9642
Unpaired FM - Paired FM	-0.1427	0.0098	803.74	-14.529	<0.0001
Unpaired FF/MM - Paired FM	-0.1410	0.0098	804.26	-14.358	<0.0001

F: female, M: male

CrossCorr8_50&100%Pairs ~ PercentPair + Paired + Distance + PercentPair:Distance, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.75

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0011	0.0335
Bird1ID	0.0015	0.0396
Bird2ID	0.0015	0.0393
RepetitionNB	6.291e-05	0.0079
Residual	0.0020	0.0448

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.1553	0.0241	5.9	-47.799	<0.0001
PercentPair100	-0.0425	0.0320	5.9	-1.329	0.2328
PairedYes	0.0342	0.017	521.3	2.013	0.0446
Dist2	-0.0470	0.0079	610.9	-5.915	<0.0001
Dist3	-0.0510	0.0085	635.1	-5.941	<0.0001
Dist4	-0.0522	0.0098	623.7	-5.287	<0.0001
PercentPair:PairedYes	0.0850	0.0211	543.5	4.02	<0.0001
PercentPair100:Dist2	0.0260	0.0113	604.6	2.292	0.0223
PercentPair100:Dist3	0.0131	0.0123	632.1	1.068	0.2861
PercentPair100:Dist4	0.0121	0.0138	617.7	0.874	0.3825

*Pairwise comparisons Paired * Dist (Tukey adjustment):*

Contrast	Estimate	SE	df	tratio	pvalue
Unpaired Dist1 - Paired Dist1	-0.0935	0.0112	840.74	-8.313	<0.0001

Table 6

MeanTransitionProba4 ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.70

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0002	0.0164
Bird1ID	0.0059	0.0769
Bird2ID	0.0059	0.0769
RepetitionNB	0.0000	0.0000
Residual	0.0062	0.0791

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-1.0009	0.0320	34.9	-31.193	<0.0001
PercentPair50	0.0039	0.0460	34.6	0.085	0.9328
PercentPair100	-0.0116	0.0372	32.9	-0.313	0.7563
UnPairedNeighb	0.0243	0.0079	420.5	3.051	0.0024
PairedNeighb	0.1477	0.0106	429.8	13.914	<0.0001

Multiple comparisons PairedNeighb (Tukey adjustment):

Contrast	Estimate	StdError	z-value	pvalue
UnPairedNeighb - UnPairedNonNeighb	0.0243	0.0079	3.051	0.0062
PairedNeighb - UnPairedNonNeighb	0.1477	0.0106	13.914	<0.0001
PairedNeighb - UnPairedNeighb	0.1233	0.0109	11.286	<0.0001

MeanTransitionProba8 ~ PercentPair + PairedNeighb, random=GroupID, RepetitionNb, Bird1, Bird2

R2c = 0.68

Random effects:

Groups Name	Variance	Std.Dev.
GroupID	0.0000	0.0000
Bird1ID	0.0248153	0.15753
Bird2ID	0.0248153	0.15753
RepetitionNB	0.0001199	0.01095
Residual	0.0279268	0.16711

Fixed effects:

	Estimate	Std. Error	df	tvalue	pvalue
(Intercept)	-2.154	0.0463	139.6	-46.5	<0.0001
PercentPair50	-0.0260	0.065	138.1	-0.401	0.689
PercentPair100	-0.0631	0.0608	138.7	-1.037	0.301
UnPairedNeighb	0.1013	0.0093	1862	10.85	<0.0001

Supp Figure1

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Supp Figure2

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Supp Figure3

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Supp Figure4

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